

First host plant record for *Pacarina* (Hemiptera, Cicadidae)

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Academic editor: P. Nunes-Silva | Received 4 December 2019 | Accepted 20 February 2020 | Published 19 March 2020

Citation: Aiello A, Stucky BJ (2020) First host plant record for *Pacarina* (Hemiptera, Cicadidae). Neotropical Biology and Conservation 15(1): 77–88. <https://doi.org/10.3897/neotropical.15.e49013>

Abstract

Twenty-nine *Pacarina* (Hemiptera: Cicadidae) adults, 12 males and 17 females, emerged from the soil of a potted *Dracaena trifasciata* (Asparagaceae) in Arraiján, Republic of Panama, providing the first rearing records and the first definitive host plant records for any species of *Pacarina*. These reared *Pacarina* appear to be morphologically distinct from all known species of *Pacarina* and likely represent an undescribed species. In light of this finding, we also discuss the taxonomy, biogeography, and ecology of *Pacarina*.

Keywords

cicada, *Dracaena*, host plant, rearing, taxonomy

Introduction

As far as is known, all cicadas are herbivores that spend the vast majority of their long life cycles as nymphs, living deep underground and feeding on the xylem sap of plant roots (Beamer 1928; Cheung and Marshall 1973; White and Strehl 1978). Because of their relative inaccessibility to researchers, very little information is available about the host plant associations of juvenile cicadas. Consequently, even though adult cicadas are among the most conspicuous and familiar of all insects, the host plants of most cicada species' nymphs remain unknown.

Positive rearing records are one of the few ways to establish with certainty which plants are suitable hosts for a particular cicada species. Although many species have been broadly associated with particular plant communities or ecoregions (e.g., Tinkham 1941; Young 1980; Kondratieff et al. 2002; Phillips and Sanborn 2007; Sanborn and Phillips 2013), such data can only suggest potential hosts. Records of which plant species female cicadas choose for oviposition are undoubtedly more useful, but oviposition sites do not necessarily match the plant species on which the nymphs will eventually feed (Newell 1906; Beamer 1928).

Unfortunately, cicada nymphs are quite difficult to maintain in captivity (Beamer 1928; Myers 1929; Moulds 1990), and this, combined with their long, multi-year life cycles, means that few researchers have attempted to rear them. Among the hundreds of species of Nearctic and Neotropical cicadas, we are aware of rearing records for only about a dozen species, nearly all from North America (Table 1). Furthermore, of these, nearly all were partial rearings that covered only one or a few nymphal instars. Only *Diceroprocta apache* Davis, *Magicicada sp.*, and *Quesada gigas* (Olivier) have been successfully reared from egg to adult (Table 1).

We report here the first known captive rearing of the genus *Pacarina* Distant (1905b). Cicadas identified as *Pacarina* nr. *puella* Davis (1923) were reared in central Panama on the host plant *Dracaena trifasciata* (Prain) Mabb. (Asparagales: Ruscaceae). Because *Dracaena trifasciata* is not native to the Americas, our results clearly represent a novel host relationship for this cicada. Furthermore, although the cicadas reared in this study are morphologically similar to *Pacarina puella*, there is reason to believe that they represent an undescribed species, so we also discuss the taxonomy of the genus and previously published records of *Pacarina* in Panama.

Methods

When exuviae from six cicada nymphs were found on a potted *D. trifasciata* plant kept on AA's front porch, it was decided to enclose the plant, pot and all, in a window screen and hardware cloth cage (Fig. 1) [photos P01878-P01880 taken 29 December 2006].

The window screen was sewn into a cylinder with fishing line, and reinforced by an external hardware cloth cylinder sewn with wire. The cage was capped with the cover from a white plastic 5-gallon tank. The finished cage was 29.2 cm (11.5") in diameter and 91.4 cm (36") high. The diameter was chosen to fit the tank cover. The height corresponded to the original width of the hardware cloth.

Exuviae were pointed. Adults were captured in vials and frozen, and later pinned. All specimens are labeled as Aiello lot 2006-25, plus an individual number. When two or more individuals of the same sex emerged on the same day and it wasn't possible to match the exuviae to their adults, the exuviae were labeled with all possible individual numbers. Individual #7 (male) and its exuviae were deposited in MIUP (*Museo de Invertebrados G. B. Fairchild de la Universidad de Panamá*), individual #8 (male) and its exuviae were deposited at the University of Colorado Museum of

Table 1. Published rearing records of Nearctic and Neotropical cicada species. “Rearing type” indicates whether rearing was complete from egg to adult (“C”) or a partial rearing that included only one or a few nymphal stadia (“P”).

Cicada species	Rearing type	References
<i>Cicadetta calliope</i> (Walker)	P	(Beamer 1928)
<i>Diceroprocta apache</i> Davis	C	(Ellingson et al. 2002)
<i>D. vitripennis</i> (Say)	P	(Beamer 1928)
<i>Hadoa bifida</i> (Davis)	P	(Beamer 1928)
<i>Magicicada</i> sp.	C, P	(Marlatt 1907; Beamer 1928; Karban et al. 2000)
<i>Magicicada tredecassini</i> Alexander & Moore	P	(English et al. 2006)
<i>Megatibicen dealbatus</i> (Davis)	P	(Beamer 1928)
<i>Megatibicen dorsatus</i> (Say)	P	(Beamer 1928)
<i>Megatibicen pronotalis</i> (Davis)	P	(Beamer 1928)
<i>Neocicada hieroglyphica</i> (Say)	P	(Beamer 1928)
<i>Neotibicen auriferus</i> (Say)	P	(Beamer 1928)
<i>Neotibicen pruinosus</i> (Say)	P	(Beamer 1931)
<i>Quesada gigas</i> (Olivier)	C, P	(Kubota 2013; Andrade 2018)

Natural History, and the remaining reared specimens are in the Aiello collection at the Smithsonian Tropical Research Institute, Panama (STRI).

Other material examined were 25 specimens at STRI. Of these, 23 are in the Henk Wolda Collection, and two are in the STRI Synoptic Collection. The two Synoptic Collection specimens were collected at a UV light on Barro Colorado Island (BCI). Among the Wolda specimens, 21 were captured in light traps at three locations: Las Cumbres, BCI, and Coco Solo Hospital. The other two Wolda specimens are from a Malaise Trap in Curundu, and from the canopy on Pipeline Road. The early Wolda material was determined by Michel Boulard in 1975. Later Wolda specimens have not yet been examined critically. The reared specimens at STRI were determined by BJS. To aid in determination, we compared the reared specimens of *Pacarina* to high-resolution images of the type specimens of *Cicada signifera* Walker (1858; = *Pacarina puella* Davis) and *Pacarina schumanni* Distant (1905a), both housed in the Natural History Museum, London.

Results

The original three cicada nymphal exuviae (2 male, 1 female) were found 16 December 2006, on the leaves of a potted *D. trifasciata* plant on AA’s front porch, Panamá: Arraiján, Loma del Río (8.9407N, 79.6568W; elevation ~154 m). They were followed by two more (1 male, 1 female) on 22 December, and a sixth (female) on 23 December. Each nymph had climbed a leaf to a point several centimeters above the soil, and anchored itself by grasping the rigid leaf margin with the legs of one side of its body, and hooking the tarsi of the opposite side into the smooth leaf surface.

Because the pot was isolated by several meters from any other soil, except for that of a potted *Calathea veitchiana* J. H. Veitch ex Hook. f. (Marantaceae), 5 meters

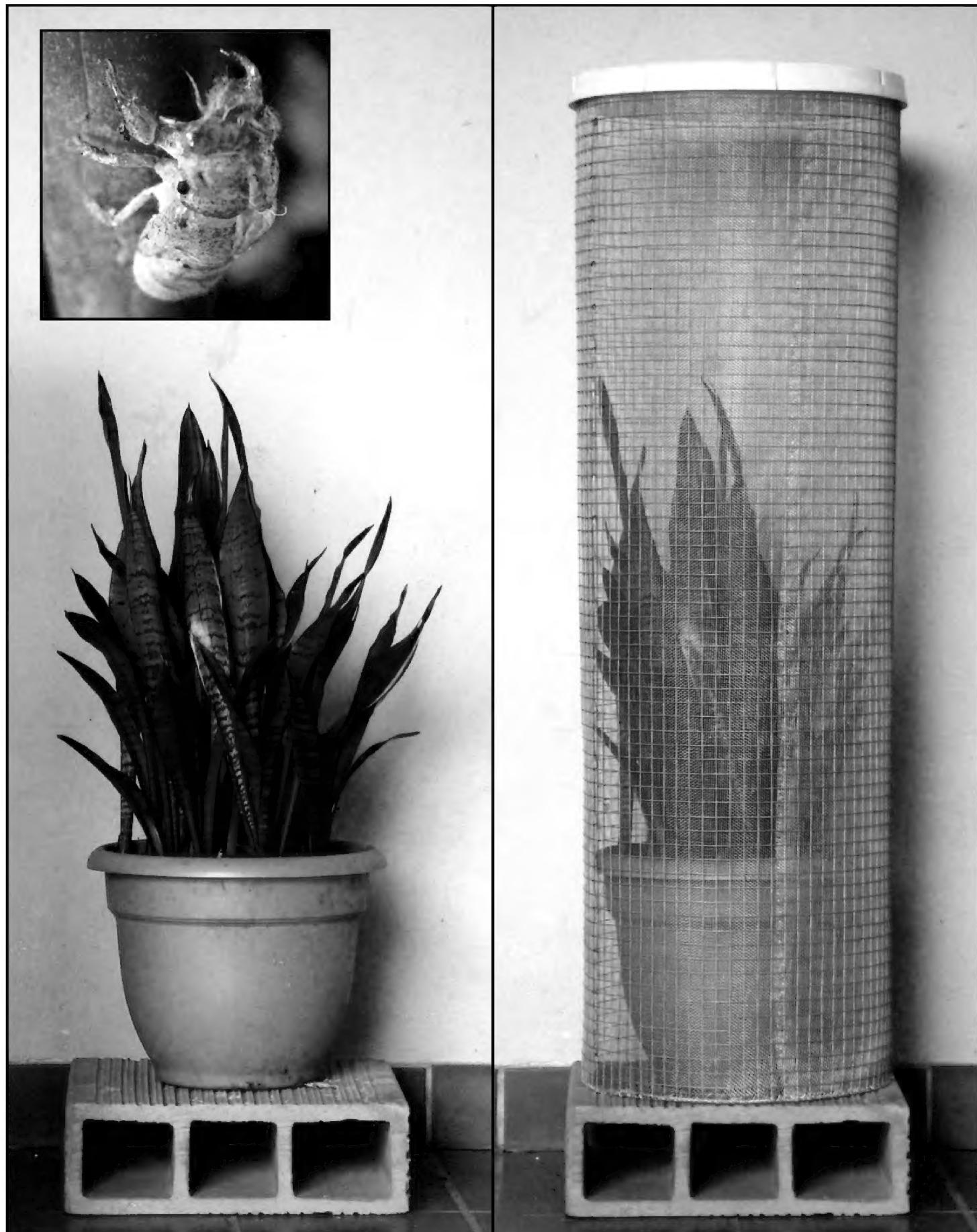


Figure 1. Cage to capture cicadas, *Pacarina sp.*, emerging from soil, where they fed on *Dracaena trifasciata* roots (left image: host plant without cage; right image: host plant with cage), with exuviae from an emerged cicada photographed *in situ* (inset image). Panama: Arraiján, Loma del Río, 29 December 2006. Aiello lot 2006-25.

away, on which no exuviae ever were found, it was obvious that the cicadas truly were associated with the *D. trifasciata* plant. This became even more obvious when, after the cage was installed, 21 additional adults emerged.

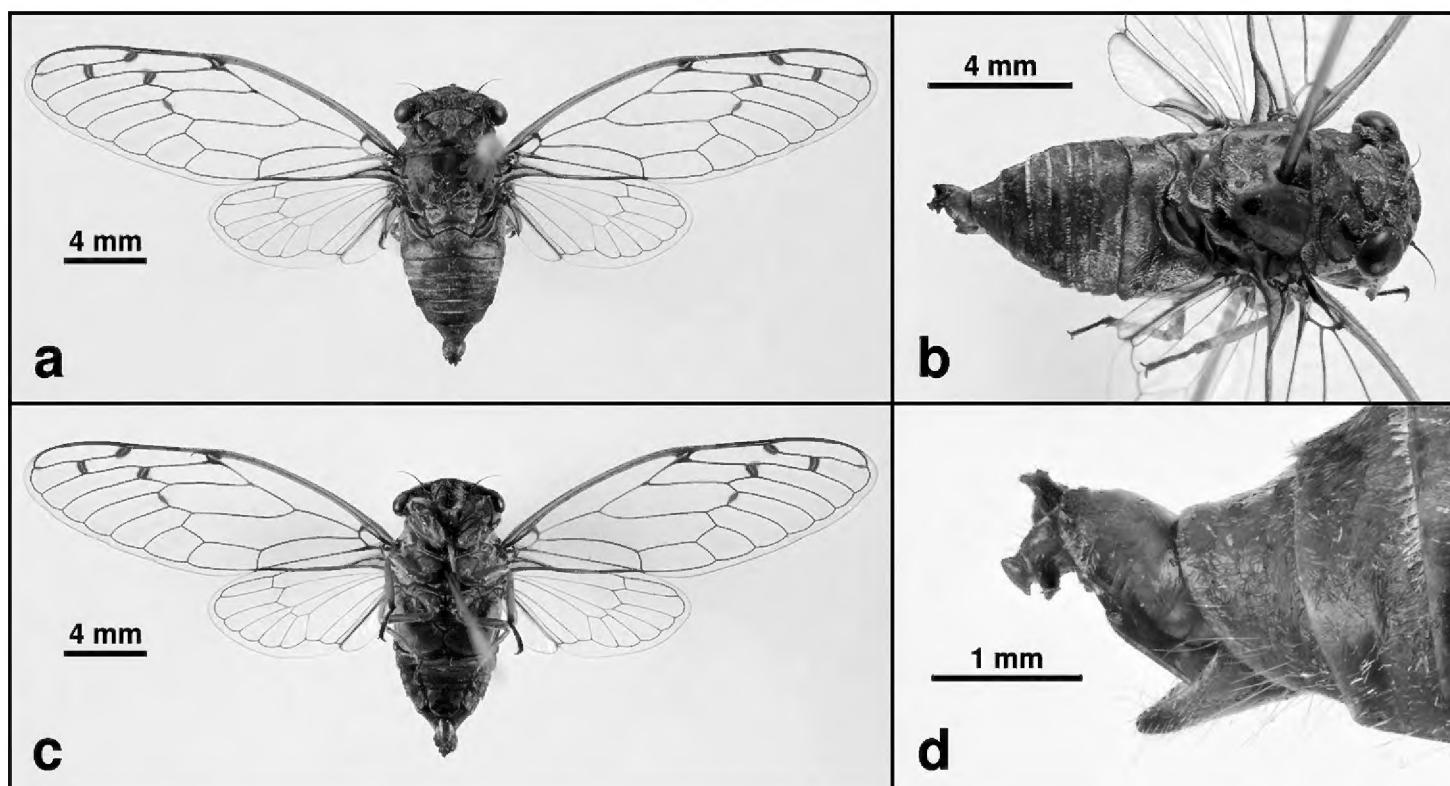


Figure 2. Male *Pacarina* sp. reared from *Dracaena trifasciata*: a) dorsal view; b) dorsolateral view; c) ventral view; d) lateral view of terminalia. This specimen is individual #8 in Table 2.

The only individual for which we have a precise emergence time is #22, which surfaced as AA watched at 09:31 hours. Its wings expanded in a matter of seconds. Three other individuals had preceded it, possibly minutes before, because they were positioned among the leaf bases and were rather inactive. It is our impression that adults emerge in the morning and stay among the leaf bases and don't move into the upper area of the cage until much later. Usually they were found near the top of the cage in late afternoon or early evening.

The cage was removed on 3 February 2007 because no eclosions had occurred since 14 January 2006. However, two more (#28 and #29, both females) did emerge on 7 February and we have their exuviae only. In total, 29 cicadas, comprising 12 males and 17 females, emerged (Table 2).

The cicadas reared from the *D. trifasciata* clearly belonged to the genus *Pacarina*, but we could not identify them as any of the known species in the genus (Fig. 2). Instead, comparison to type material strongly suggested that our reared *Pacarina* represent an undescribed species. Of the described species of *Pacarina*, the reared *Pacarina* are most similar to *P. puella*.

Discussion

Ecology and life history of *Pacarina* in Panama

Our results provide the first definitive host plant record for any species of *Pacarina*. Although we did not directly observe any female *Pacarina* ovipositing in the potted *Dracaena trifasciata*, there is no other convincing explanation for the presence of so many nymphal *Pacarina* on the plant. It is conceivable that oviposition occurred

Table 2. Emergence dates and times for *Pacarina sp.* reared as Aiello lot 2006-25 from potted *Dra-
caena trifasciata* (Asparagaceae) in Loma del Río, Arraiján, Panama. “Catalog number” refers to the
identifier for each specimen in the Smithsonian Tropical Research Institute’s online Symbiota collec-
tions data portal, accessible at <https://stricollections.org/portal/collections/index.php>.

Individual	Sex	Found as	Date	Time	Catalog number
1	♂	exuviae	16 Dec. 2006	?	STRI_ENT_0121962
2	♀	exuviae	16 Dec. 2006	?	STRI_ENT_0121964
3	♂	exuviae	16 Dec. 2006	?	STRI_ENT_0121966
4	♀	exuviae	22 Dec. 2006	?	STRI_ENT_0121963
5	♂	exuviae	22 Dec. 2006	?	STRI_ENT_0121965
6	♀	exuviae	23 Dec. 2006	?	STRI_ENT_0121967
7	♂	adult	24 Dec. 2006	19:15	STRI_ENT_0121968
7	♂	exuviae	24 Dec. 2006	19:15	STRI_ENT_0121969
8	♂	adult	25 Dec. 2006	19:21	STRI_ENT_0121970
8	♂	exuviae	25 Dec. 2006	19:21	STRI_ENT_0121971
9	♀	adult	26 Dec. 2006	18:39	STRI_ENT_0121972
9	♀	exuviae	26 Dec. 2006	18:39	STRI_ENT_0121973
10	♂	adult	27 Dec. 2006	19:35	STRI_ENT_0121974
11	♂	adult	27 Dec. 2006	19:35	STRI_ENT_0121975
10/11	♂	exuviae	27 Dec. 2006	19:35	STRI_ENT_0121976
10/11	♂	exuviae	27 Dec. 2006	19:35	STRI_ENT_0121977
12	♂	adult	28 Dec. 2006	19:09	STRI_ENT_0121978
12	♂	exuviae	28 Dec. 2006	19:09	STRI_ENT_0121979
13	♀	adult	28 Dec. 2006	19:09	STRI_ENT_0121980
14	♀	adult	28 Dec. 2006	19:09	STRI_ENT_0121981
13/14	♀	exuviae	28 Dec. 2006	19:09	STRI_ENT_0121982
13/14	♀	exuviae	28 Dec. 2006	19:09	STRI_ENT_0121983
15	♀	adult	29 Dec. 2006	19:36	STRI_ENT_0121984
16	♀	adult	29 Dec. 2006	19:36	STRI_ENT_0121985
15/16	♀	exuviae	29 Dec. 2006	19:36	STRI_ENT_0121986
15/16	♀	exuviae	29 Dec. 2006	19:36	STRI_ENT_0121987
17	♂	adult	02 Jan. 2007	<12:00	STRI_ENT_0121988
18	♂	adult	02 Jan. 2007	<12:00	STRI_ENT_0121989
19	♂	adult	03 Jan. 2007	<09:31	STRI_ENT_0121990
17/18/19	♂	exuviae	03 Jan. 2007	<09:31	STRI_ENT_0121991
17/18/19	♂	exuviae	03 Jan. 2007	<09:31	STRI_ENT_0121992
17/18/19	♂	exuviae	03 Jan. 2007	<09:31	STRI_ENT_0121992
20	♀	adult	03 Jan. 2007	<09:31	STRI_ENT_0121994
21	♀	adult	03 Jan. 2007	<09:31	STRI_ENT_0121995
20/21	♀	exuviae	03 Jan. 2007	<09:31	STRI_ENT_0121996
20/21	♀	exuviae	03 Jan. 2007	<09:31	STRI_ENT_0121997
22	♀	adult	03 Jan. 2007	09:31	STRI_ENT_0121998
22	♀	exuviae	03 Jan. 2007	09:31	STRI_ENT_0121999
23	♂	adult	04 Jan. 2007	morning	STRI_ENT_0122000
23	♂	exuviae	04 Jan. 2007	morning	STRI_ENT_0122001
24	♀	adult	04 Jan. 2007	19:42	STRI_ENT_0122002
24	♀	exuviae	04 Jan. 2007	19:42	STRI_ENT_0122003
25	♀	adult	08 Jan. 2007	<09:30	STRI_ENT_0122004
25	♀	exuviae	08 Jan. 2007	<09:30	STRI_ENT_0122005
26	♀	adult	14 Jan. 2007	morning	STRI_ENT_0122006
26/27	♀	exuviae	14 Jan. 2007	morning	STRI_ENT_0122007
27	♀	adult	14 Jan. 2007	?	escaped
26/27	♀	exuviae	14 Jan. 2007	?	STRI_ENT_0122010
28	♀	exuviae	06 Feb. 2007	?	STRI_ENT_0122008
29	♀	exuviae	06 Feb. 2007	?	STRI_ENT_0122009

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elsewhere and the hatchling cicadas were carried to the *D. trifasciata* by the wind, but given the pot's relative isolation from any nearby vegetation and the large number of cicadas that emerged from it, this is highly unlikely. In any case, there can be no doubt that the *D. trifasciata* was the food source for the developing nymphs.

Dracaena Vand. ex L. (Asparagaceae, but formerly of the Ruscaceae) is a genus of about 60 species of both terrestrial and epiphytic plants, mostly from Africa and south Asia, with two species endemic to the Neotropics and only one, *D. americana* Donn. Sm., a tree, found in Central America, including Panama (Zona et al. 2014). In Panama, *D. americana* appears to be limited to the extreme western part of the country (Zona et al. 2014). If we assume that *D. trifasciata* is at least distantly related to the natural host plants of the reared *Pacarina* species, the most likely candidates in Panama include three *Agave* species (*angustifolia*, *hurteri*, *seemanniana*) and *Furcraea cabuya*, all belonging to the Asparagaceae (s.l.). *D. trifasciata* is terrestrial and is native to South Africa. It is among the most popular pot plants worldwide.

Though no information is available about native hosts in Panama, Young (1974) studied the possible host relationships of *Pacarina* in grasslands in western Costa Rica. He observed that nymphal exuviae were found among patches of *Rhynchospora* (= *Dichromena*) *ciliata* (Vahl) (Cyperaceae) and inferred that this sedge was the probable food plant. The only similarity between *Dracaena* and *Rhynchospora* is that both are monocots, which could be a significant relationship in this case. Young did not identify the species of *Pacarina* he studied and suspected that it was undescribed.

The *Pacarina* in our study eclosed over a 53-day period from December 16, 2006 to February 6, 2007, but 21 of the 29 total individuals ($\approx 72\%$) eclosed during the 14 days from December 22 to January 4. This timing matches well with the emergence phenology of *P. puella* in Las Cumbres (Wolda and Ramos 1992), a lowland residential area in south central Panama that is only ~ 20 km away from our study location and expected to have qualitatively similar habitat.

The total life cycle length of the reared *Pacarina* is unknown. However, the *D. trifasciata* on which the cicadas were reared was divided from a parent plant and repotted on 5 August 2005. No cicada nymphs were observed in the soil at that time, although it is possible that early instars were present and overlooked due to their small size. We think that is unlikely, though, for two reasons. First, early stage cicada nymphs are extremely fragile and vulnerable to desiccation (Beamer 1928) and could have easily been killed while dividing and re-potting the parent plant. Second, no cicadas are known to have emerged from any of the other plants derived from the original parent, which strongly suggests that no cicada nymphs were present on the roots of the parent plant. If the nymphs entered the soil after the parent plant was divided, this places an upper bound of 498 days on the nymphal development time of the earliest-emerging cicadas. Assuming that all of the reared *Pacarina* derived from the same oviposition event, the 53 days between the first and last adult cicada eclosions indicates considerable variability in egg and/or nymphal development times for this species of *Pacarina*.

Taxonomy and biogeography of *Pacarina*

The genus *Pacarina* is distributed from the southwestern United States (US) southward through Central America, including Panama, and presently comprises three described species: *puella* Davis, *schumanni* Distant, and *shoemakeri* Sanborn & Heath (Sanborn et al. 2012; Sanborn 2018). All three species are small cicadas that resemble each other in general appearance. Two species, *P. puella* and *P. schumanni*, have previously been recorded from Panama (Sanborn 2018). *Pacarina puella* is reported as the most widespread species in the genus, having been collected as far north as the state of Oklahoma in the US, in Mexico, and in Central America as far south as Panama (Drew et al. 1974; Wolda and Ramos 1992; Sanborn et al. 2012).

Although the recent key to *Pacarina* published by Sanborn et al. (2012) would identify our specimens as *P. schumanni*, the wing morphology does not match Distant's description (1905a) and the general habitus and genitalia are markedly different from that of the *P. schumanni* holotype. Similarly, the terminalia of the holotype of *P. puella* differ from those of the reared specimens, especially in the form of the pygofer and uncus. The northern geographic range and restricted habitat requirements of *P. shoemakeri* (Sanborn et al. 2012) exclude it as a possibility.

Until more complete data are available for *Pacarina* in Panama and elsewhere in Central and North America, we prefer not to describe our specimens as a new species and risk further confusion. More complete morphological, ecological, and bioacoustic data for *P. puella* and *P. schumanni* from at or near their type localities would be especially useful, as would a reexamination of existing specimens in various collections. The labels from the holotype of *P. schumanni* give the collecting locality as "Atoyac, Vera Cruz" but the labels from the holotype of *P. puella* only state that the collecting locality was "Mex." However, Walker, in his original description of *Cicada signifera* (= *P. puella*), reported "Orizaba, Mexico" as the holotype locality (Walker 1858). These two type localities are both near the western border of the modern Mexican state of Veracruz, separated by only about 35 km. We were unable to examine any other specimens of *P. puella* or *P. schumanni* from these locations, and no ecological or bioacoustic data is available for either species from their type localities. Sueur (2002) studied *P. schumanni* in eastern Veracruz, but virtually all published natural history information for *P. puella* comes either from the northern limit of its range in the United States or the southern limit of its range in Panama. Bioacoustic data would be particularly valuable, because cicada species' unique calls provide the single most important mechanism for pre-zygotic reproductive isolation (Alexander and Moore 1958; Boulard 2006) and there are numerous examples of morphologically cryptic cicada species that are most easily distinguished by their calling songs (e.g., Davis 1922; Alexander and Moore 1962; Popov 1989; Marshall and Cooley 2000; Quaratau and Simões 2005; Sueur and Puissant 2007; Cole 2008; Gogala et al. 2008; Popple 2013; Stucky 2013; Ewart 2018).

We also note that the striking ecological divergence between northern and southern populations of *P. puella* suggests that *P. puella*, as currently recognized,

might not even be a single species. In North America, *P. puella* is typically found in relatively dry habitats on or near mesquite (Fabaceae: *Prosopis* spp.) (Davis 1917, Sanborn et al. 2012, Sanborn and Phillips 2013), which led Sanborn et al. (2012) to conclude that mesquite was its host plant. In fact, this ecological association is one of the diagnostic features that separate *P. puella* from the recently-described *P. shoemakeri*, which instead is found primarily on junipers (Sanborn et al. 2012). Although at least one species of *Prosopis* does occur in Panama (Condit et al. 2011), *Prosopis* evidently is not found on Barro Colorado Island (Croat 1978), where cicadas that have been identified as *P. puella* are nevertheless relatively common (Wolda 1989). Either *Prosopis* is not an obligate host for *P. puella* or the northern and southern populations represent different species, either of which *might* be true *P. puella*. Again, a critical re-examination of previous literature records for *Pacarina*, combined with more thorough ecological and bioacoustic data, are needed to properly resolve the taxonomy of this genus.

Conclusions

Our results provide the first definitive host plant record for any species of *Pacarina*, and one of the few captive rearing records for any species of cicada. The cicadas we reared appear to be an undescribed species. We suggest three directions for future work on *Pacarina*. First, it would be useful to ascertain the host plants of “*P. puella*” in both the US and Panama. In particular, does *P. puella* in the US actually use mesquite as a host, or is the relationship merely coincidental? We have demonstrated that *Pacarina* can be reared in a relatively small space, so future investigations of potential host plants should be feasible by enclosing females with candidate plants to see whether they oviposit, and if so, whether the nymphs successfully develop on them. Second, more complete morphological and bioacoustic data for *P. puella* and *P. schumanni*, especially from their type localities, are needed to facilitate a critical re-evaluation of previous literature records of *Pacarina* and to determine the status of purported *P. puella* in the US and Panama. Third, molecular data from representative specimens throughout the geographic range of *Pacarina* could be used to provide a phylogenetic context for interpreting morphological, ecological, and bioacoustic data and to further guide species delimitation. Together, these data would allow us to finally untangle the taxonomy of these enigmatic little cicadas.

Acknowledgments

We are grateful to Ricardo Cortez for technical advice and help with building the cage and to Edwin Ernesto Domínguez Núñez for technical assistance. We also thank Mick Webb and Tatiana Ruschel for providing photographs of the holotype specimens of *P. puella* and *P. schumanni*. Paula Simões and an anonymous reviewer provided helpful comments on the manuscript. BJS gratefully acknowledges the support of a 2013 Smithsonian Tropical Research Institute short-term fellowship.

References

Alexander RD, Moore TE (1958) Studies on the acoustical behavior of seventeen-year cicadas. *The Ohio Journal of Science* 58: 107–127.

Alexander RD, Moore TE (1962) The evolutionary relationships of 17-year and 13-year cicadas, and three new species. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 121: 1–59.

Andrade S de C (2018) Aspectos Bioecológicos de *Quesada gigas* (Olivier, 1790) (Hemiptera: Cicadidae) Associados à Cultura do Café. Universidade Estadual Paulista. https://repositorio.unesp.br/bitstream/handle/11449/180359/andrade_sc_dr_jabo.pdf

Beamer RH (1928) Studies on the biology of Kansas Cicadidae. *The University of Kansas Science Bulletin* 18: 155–263.

Beamer RH (1931) Notes on the emergence of *Tibicen pruinosa* (Say) (Homoptera-Cicadidae). *Journal of the Kansas Entomological Society* 4: 51–52.

Boulard M (2006) Acoustic signals, diversity and behaviour of cicadas (Cicadidae, Hemiptera). In: Drosopoulos S, Claridge M (Eds) *Insect Sounds and Communication: Physiology, Behaviour, Ecology and Evolution*. CRC Press, Boca Raton, 331–349. <https://doi.org/10.1201/9781420039337.ch25>

Cheung WWK, Marshall AT (1973) Water and ion regulation in cicadas in relation to xylem feeding. *Journal of Insect Physiology* 19(9): 1801–1816. [https://doi.org/10.1016/0022-1910\(73\)90049-8](https://doi.org/10.1016/0022-1910(73)90049-8)

Cole JA (2008) A new cryptic species of cicada resembling *Tibicen dorsatus* revealed by calling song (Hemiptera: Auchenorrhyncha: Cicadidae). *Annals of the Entomological Society of America* 101(5): 815–823. <https://doi.org/10.1093/aesa/101.5.815>

Condit R, Pérez R, Daguerre N (2011) *Trees of Panama and Costa Rica*. Princeton University Press, Princeton, 494 pp. <https://doi.org/10.1515/9781400836178>

Croat TB (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, 943 pp.

Davis WT (1917) Sonoran cicadas collected by Harry H. Knight, Dr. Joseph Bequaert and others, with descriptions of new species. *Journal of the New York Entomological Society* 25: 203–215.

Davis WT (1922) An annotated list of the cicadas of Virginia with description of a new species. *Journal of the New York Entomological Society* 30: 36–52.

Davis WT (1923) Notes on North American cicadas with descriptions of new species. *Journal of the New York Entomological Society* 31: 1–15.

Distant WL (1905a) Appendix. *Biologia Centrali-Americana. Rhynchota Homoptera* 1: 140–147.

Distant WL (1905b) Rhynchotal notes.—XXX. *Annals and Magazine of Natural History, Seventh Series* 15: 304–319. <https://doi.org/10.1080/03745480509443047>

Drew WA, Spangler FL, Molnar D (1974) Oklahoma Cicadidae (Homoptera). *Proceedings of the Oklahoma Academy of Science* 54: 90–97.

Ellingson AR, Andersen DC, Kondratieff BC (2002) Observations of the larval stages of *Diceroprocta apache* Davis (Homoptera: Tibicinidae). *Journal of the Kansas Entomological Society* 75: 283–289.

English LD, English JJ, Dukes RN, Smith KG (2006) Timing of 13-year periodical cicada (Homoptera: Cicadidae) emergence determined 9 months before emergence. *Environmental Entomology* 35(2): 245–248. <https://doi.org/10.1603/0046-225X-35.2.245>

Ewart A (2018) Two new genera and five new species of *Mugadina*-like small grass cicadas (Hemiptera: Cicadidae: Cicadettini) from Central and Eastern Australia: comparative morphology, songs, behaviour and distributions. *Zootaxa* 4413(1): 1. <https://doi.org/10.11646/zootaxa.4413.1.1>

Gogala M, Drosopoulos S, Trilar T (2008) *Cicadetta montana* complex (Hemiptera, Cicadidae) in Greece – a new species and new records based on bioacoustics. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Deutsche Entomologische Zeitschrift* 55(1): 91–100. <https://doi.org/10.1002/mmnd.200800006>

Karban R, Black CA, Weinbaum SA (2000) How 17-year cicadas keep track of time. *Ecology Letters* 3(4): 253–256. <https://doi.org/10.1046/j.1461-0248.2000.00164.x>

Kondratieff BC, Ellingson AR, Leatherman DA (2002) The cicadas of Colorado. *Insects of Western North America* 2: 1–63.

Kubota MM (2013) Aspectos Biológicos de *Quesada gigas* (Olivier, 1790) (Hemiptera: Cicadidae) em Cafeeiro. Universidade Estadual Paulista. <https://repositorio.unesp.br/bitstream/handle/11449/91306/000725837.pdf>

Marlatt CL (1907) The periodical cicada. *Bulletin of the Bureau of Entomology of the U.S. Department of Agriculture* 71: 5–181. <https://doi.org/10.5962/bhl.title.109956>

Marshall DC, Cooley JR (2000) Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution; International Journal of Organic Evolution* 54(4): 1313–1325. <https://doi.org/10.1111/j.0014-3820.2000.tb00564.x>

Moulds MS (1990) Australian Cicadas. New South Wales University Press, Kensington, 217 pp.

Myers JG (1929) Insect Singers: A Natural History of the Cicadas. George Routledge and Sons, London, 304 pp.

Newell W (1906) Notes upon a little-known insect enemy of cotton and corn. *Bulletin of the Bureau of Entomology of the U.S. Department of Agriculture* 60: 52–58.

Phillips PK, Sanborn AF (2007) Phytogeography influences biogeography of the Cicadidae. *Dong Wu Xue Bao* 53: 454–462.

Popov AV (1989) Species of singing cicadas revealed on the basis of peculiarities of acoustic behavior. 1. *Cicadatra cataphractica* Popov (ex. gr. *Querula*) (Homoptera, Cicadidae). *Entomological Review* 68: 62–78.

Popple LW (2013) A revision of the *Pauropsalta annulata* Goding & Froggatt species group (Hemiptera: Cicadidae) based on morphology, calling songs and ecology, with investigations into calling song structure, molecular phylogenetic relationships and a case of hybridisation between two subspecies. *Zootaxa* 3730(1): 1. <https://doi.org/10.11646/zootaxa.3730.1.1>

Quartau JA, Simões PC (2005) *Cicada cretensis* sp. n. (Hemiptera, Cicadidae) from southern Greece. *Biologia* 60: 489–494.

Sanborn AF (2018) The cicadas (Hemiptera: Cicadidae) of Panama including the description of six new species, three new combinations, one new synonymy, and nine new records. *Zootaxa* 4493(1): 1. <https://doi.org/10.11646/zootaxa.4493.1.1>

Sanborn A, Phillips P (2013) Biogeography of the cicadas (Hemiptera: Cicadidae) of North America, north of Mexico. *Diversity (Basel)* 5(2): 166–239. <https://doi.org/10.3390/d5020166>

Sanborn AF, Heath MS, Phillips PK, Heath JE (2012) The genus *Pacarina* Distant, 1905 (Hemiptera: Cicadidae) with the description of a new species. *Journal of Natural History* 46(15–16): 923–941. <https://doi.org/10.1080/00222933.2011.651647>

Stucky BJ (2013) Morphology, bioacoustics, and ecology of *Tibicen neomexicensis* sp. n., a new species of cicada from the Sacramento Mountains in New Mexico, U.S.A. (Hemiptera, Cicadidae, *Tibicen*). *ZooKeys* 337: 49–71. <https://doi.org/10.3897/zookeys.337.5950>

Sueur J (2002) Cicada acoustic communication: potential sound partitioning in a multi-species community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society. Linnean Society of London* 75(3): 379–394. <https://doi.org/10.1111/j.1095-8312.2002.tb02079.x>

Sueur J, Puissant S (2007) Similar look but different song: A new *Cicadetta* species in the *montana* complex (Insecta, Hemiptera, Cicadidae). *Zootaxa* 1442(1): 55–68. <https://doi.org/10.11646/zootaxa.1442.1.5>

Tinkham ER (1941) Biological and faunistic notes on the Cicadidae of the Big Bend region of Trans-Pecos Texas. *Journal of the New York Entomological Society* 49: 165–183.

Walker F (1858) List of the Specimens of Homopterous Insects in the Collection of the British Museum: Supplement. Edward Newman, London, 369 pp.

White J, Strehl CE (1978) Xylem feeding by periodical cicada nymphs on tree roots. *Ecological Entomology* 3(4): 323–327. <https://doi.org/10.1111/j.1365-2311.1978.tb00933.x>

Wolda H (1989) Seasonal cues in tropical organisms. Rainfall? Not necessarily! *Oecologia* 80(4): 437–442. <https://doi.org/10.1007/BF00380064>

Wolda H, Ramos JA (1992) Cicadas in Panama: their distribution, seasonality, and diversity (Homoptera: Cicadoidea). In: Quintero D, Aiello A (Eds) *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, Oxford, 271–279.

Young AM (1974) The population biology of Neotropical cicadas III: Behavioral natural history of *Pacarina* in Costa Rican grasslands. *Entomological News* 85: 239–256.

Young AM (1980) Habitat and seasonal relationships of some cicadas (Homoptera: Cicadidae) in central Costa Rica. *American Midland Naturalist* 103(1): 1–155. <https://doi.org/10.2307/2425049>

Zona S, de Zayas AA, Orellana R, Oviedo R, Jestrow B, Francisco-Oregia J (2014) *Dracaena* L. (Asparagaceae) in the New World: Its history and botany. *Vieraea* 42: 219–240.